

ANNALS OF THE SOUTH AFRICAN MUSEUM
ANNALE VAN DIE SUID-AFRIKAANSE MUSEUM

Volume 86 Band
October 1981 Oktober
Part 4 Deel



CRETACEOUS FAUNAS FROM
ZULULAND AND NATAL, SOUTH AFRICA
ADDITIONAL OBSERVATIONS ON THE
AMMONITE SUBFAMILY TEXANITINAE
COLLIGNON, 1948

By

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&
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Cape Town Kaapstad

The ANNALS OF THE SOUTH AFRICAN MUSEUM

are issued in parts at irregular intervals as material
becomes available

Obtainable from the South African Museum, P.O. Box 61, Cape Town 8000

Die ANNALE VAN DIE SUID-AFRIKAANSE MUSEUM

word uitgegee in dele op ongereelde tye na gelang van die
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Verkrygbaar van die Suid-Afrikaanse Museum, Posbus 61, Kaapstad 8000

OUT OF PRINT/UIT DRUK

1, 2(1-3, 5-8), 3(1-2, 4-5, 8, t.-p.i.), 5(1-3, 5, 7-9),
6(1, t.-p.i.), 7(1-4), 8, 9(1-2, 7), 10(1-3),
11(1-2, 5, 7, t.-p.i.), 15(4-5), 24(2), 27, 31(1-3), 32(5), 33, 45(1)

EDITOR/REDAKTRISE

Ione Rudner

Copyright enquiries to the South African Museum

Kopieregnavrae aan die Suid-Afrikaanse Museum

ISBN 0 86813 025 7

Printed in South Africa by
The Rustica Press, Pty., Ltd.,
Court Road, Wynberg, Cape

In Suid-Afrika gedruk deur
Die Rustica-pers, Edms., Bpk.,
Courtweg, Wynberg, Kaap

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(With 27 figures)

[MS accepted 11 June 1981]

ABSTRACT

Data supplementary to the monograph on the ammonite subfamily Texanitinae Collignon, 1948, by Klinger & Kennedy are given. These include a redescription and illustration of the type material and other Austrian and French specimens of *Ammonites serratomarginatus* Redtenbacher, 1873, and *Ammonites quinquenodosus* Redtenbacher, 1873. New material permits a study of the intraspecific variation in *Reginaites zulu* Klinger & Kennedy, 1980, and the homoeomorphy between it and *Plesiotexanites (P.) stangeri* (Baily, 1855). Two micromorph specimens of *Submortonicerias woodsi* (Spath, 1921) are homoeomorphic with *Protexanites (P.) bontanti shimizui* Matsumoto, 1970, exhibit traces of colour banding, and raise the possibility of sexual dimorphism in the subfamily Texanitinae.

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INTRODUCTION

Subsequent to Klinger & Kennedy's (1980a) monographical description of the South African representatives of the ammonite subfamily Texanitinae Collignon, 1948, additional data from South Africa and Europe became available which are supplementary to the overall account already published. Part of these were published separately (Klinger & Kennedy 1980b). Although these data deal with different and remotely related aspects of the subfamily Texanitinae, economic measures deemed it advisable to publish these under one cover with appropriate subtitles. Authorship according to seniority is given below each subtitle. Authorship for the whole publication is in alphabetical order.

LOCATION OF SPECIMENS

The following abbreviations are used to indicate the repositories of the material studied:

FSR	Faculté des Sciences, Rennes, France
GBA	Geologische Bundesanstalt, Vienna, Austria
LL	Oberösterreichisches Landesmuseum, Linz, Austria
NHMW	Naturhistorisches Museum, Vienna, Austria
NS	Haus der Natur, Salzburg, Austria
SAM	South African Museum, Cape Town, South Africa
SAS	Geological Survey of South Africa, Pretoria

DIMENSIONS OF SPECIMENS

Dimensions of specimens are given in millimetres; abbreviations are as follows:

D = diameter, Wb = whorl breadth, Wh = whorl height, U = umbilical diameter, R = ribs per whorl, U : E tbs = ratio of umbilical to external tubercles.

Figures in parentheses are dimensions as a percentage of total diameter.

SUTURE TERMINOLOGY

The suture terminology of Wedekind (1916; see Kullmann & Wiedmann 1970 for a recent review) is followed in the present work:

I = internal lobe, U = umbilical lobe, L = lateral lobe, E = external lobe.

ANNOTATION OF ORNAMENT

This follows the scheme presented in Klinger & Kennedy (1980a: 3-4); tubercles are numbered in ontogenetic sequence from the umbilical wall to the venter; e.g. umbilical tubercle is (1), lateral tubercle (2), submarginal (3), marginal (4), and external (5).

SYSTEMATIC PALAEOLOGY

ON *Ammonites serratmarginatus* REDTENBACHER, 1873. AND
Ammonites quinquenodosus REDTENBACHER, 1873.

(By W. J. Kennedy, H. Summesberger & H. C. Klinger)

Revision of the texanitid faunas of the South African Upper Cretaceous (Klinger & Kennedy 1980a) raised a number of questions, amongst others the effect of differential preservation and geographic morphological variation in *Ammonites serratmarginatus* and *Ammonites quinquenodosus*, two species from the Gosau Beds of the Austrian Alps described almost a century ago by Anton Redtenbacher (1873). It has now proved possible to locate some of the type material of these two species, as well as a series of other Austrian specimens.

Paratexanites serratmarginatus (Redtenbacher, 1873)

Figs 1–7

Ammonites serrato-marginatus Redtenbacher, 1873: 110, pl. 25 (fig. 2a–d)

Mortoniceras serrato-marginatum (Redtenbacher): De Grossouvre, 1894: 69, pl. 16 (fig. 1a–b).
Pervinquière, 1907: 242. Diener, 1925: 148.

Bevahites (*Parabevahites*) *serrato-marginatus* (Redtenbacher): Collignon, 1948: 83(38).

Non Parabevahites serrato-marginatus (Redtenbacher): Collignon, 1966: 76, pl. 486 (figs 1962–1963).

Non Parabevahites cf. *serrato-marginatus* (Redtenbacher): Collignon, 1966: 80, pl. 488 (figs 1967–1969).

Paratexanites (*Parabevahites*) *serratmarginatus* (Redtenbacher): Matsumoto, 1970: 260, pl. 36 (figs 1–3), text-fig. 16. Matsumoto & Hirano, 1976: 337, text-fig. 3.

Paratexanites (*Parabevahites*) *serratmarginatus grossouvrei* Matsumoto, 1970: 263.

Paratexanites (*Parabevahites*) cf. *serratmarginatus* (Redtenbacher): Kennedy & Kollmann, 1977: 414, pl. 1 (fig. 1a–c).

Types

Redtenbacher based this species on seven syntypes, all of which have been traced. NS 6381, the original of Redtenbacher 1873, pl. 25 (fig. 2a–b) is the lectotype; paralectotypes are NS 6376, 6379, 6387, 6384, 6385, 6387. Four further specimens may also be part of the type series: NS 18427–18428 (part and counterpart), NS 18435, LL 26590, and 26598, all from the Coniacian Gosau Beds of Glanegg, Austria.

Other specimens studied

NHMW 1978/2029/3 from the Coniacian Beds of Glanriedel, Austria, FSR 'A', Seunes Collection, FSR 2834 and 2835, all from the Coniacian Craie de Villedieu of La Ribochère, commune de Couture, Loir-et-Cher, France.

Dimensions

	<i>D</i>	<i>Wb</i>	<i>Wh</i>	<i>Wb:Wh</i>	<i>U</i>	<i>R</i>
NS 6381	45.2	16.2(38)	14.0(33)	1.15	15.0(35)	38–39?
FSR 2834	58.5	—	—	—	23.0(39)	21
FSR 'A'	72.3	—	24.5(34)	—	29.8(41)	27

Description

The lectotype (Figs 1A–C, 2I, 3B) is a small, distorted, composite internal mould just over 42 mm in diameter.

Coiling is evolute, only 25 per cent of the previous whorl being covered. The umbilicus is of moderate width (c. 35 per cent of diameter?) with a low, rounded wall. The whorl section is slightly depressed (due to post-mortem crushing), with greatest breadth below mid-flank.

Ornament consists of numerous slightly flexed, crowded prorsiradiate ribs, approximately 40 per whorl. Most arise singly from bullae (1) at the umbilical shoulder (although a few arise in pairs or are intercalated), and bear small, weakly clavate submarginal (3) and closely spaced, stronger marginal (4) tubercles. There are stronger external (5) clavi on either side of a narrow keel flanked by shallow sulci.

The earliest ontogenetic stages are seen in NS 6384 (Fig. 2G–H) and LL 26598 (Fig. 2A–B). Here, ribbing is again crowded and flexuous, with the distinctive close spacing of tubercles 3 + 4 visible even at a whorl height of only 5,5 mm. The former specimen has a compressed whorl section, presumably due to crushing, but reveals a better preserved keel than the lectotype, and this shows unmistakable undulations corresponding to the external (5) clavi. This is also seen, but is less prominent, in LL 26598, which differs from the lectotype in having the submarginal (3) tubercle longer and more prominent than the marginal (4) (Fig. 2A–B). Of the specimens corresponding in size to the lectotype, NS 18428 (NS 18427 is the counterpart) (Figs 1D, 3C) is coarser ribbed, with stronger bullae (1) and a greater forward projection to the ventrolateral ribbing. This is also seen in NS 6379 (Fig. 1I). In contrast, NS 6382 (Figs 1K, 3D), although crushed, is as densely ribbed as the lectotype.

Of the larger specimens, NS 6387, is the original of Redtenbacher 1873, pl. 25 (fig. 2C–D). It has a maximum whorl height of 20,5 mm, and appears to be sparser ribbed than the lectotype, as do all the larger specimens, suggesting outer whorls were consistently more distantly ribbed than the nuclei (Figs 1F–G, 3A). The ribs are flexuous with the submarginal (3) and marginal (4) tubercles close together, both clavate, and the former weaker than the latter (Figs 1G, 3A). The keel is well preserved, and feebly undulose. NS 6376 is identical, as far as it is preserved (Fig. 1E). In contrast, NS 18453 (Fig. 1H) shows the submarginal (3) and marginal (4) tubercles to be relatively stronger in relation to the ribs, with the submarginal (3) far more prominent, although shorter than the marginal (4). The largest and most ontogenetically advanced fragment, LL 26590 (Fig. 2C–D) shows a distinctly undulose keel and submarginal (3) and marginal (4) tubercles grouped on a swelling on the ventrolateral shoulder, with the external (5) clavi seemingly linked by weak ridges, which are much accentuated by crushing (Fig. 2D).

None of these specimens shows the sutures.



Fig. 1. *Paratexanites serratomarginatus* (Redtenbacher). A–C. The lectotype, NS 6381, the original of Redtenbacher (1873), pl. 25 (fig 2a–b). D. Paralectotype, NS 18428. E. Paralectotype, NS 6376. F–G. Paralectotype, NS 6378, the original of Redtenbacher (1873), pl. 25 (fig. 2c–d). H. Paralectotype, NS 18453. I. Paralectotype, NS 6379. J. Paralectotype, NS 6385. K. Paralectotype, NS 6382. All specimens are from the Coniacian Gosau Beds of Glanegg, Austria. $\times 1$.



Fig. 2. *Paratexanites serratomarginatus* (Redtenbacher). A-B. Paralectotype, LL 26598. C-D. Paralectotype, LL 26590. E-F. FSR 2835. G-H. Paralectotype, NS 6384. I. Lectotype, NS 6381. A-D, G-I are from the Coniacian Gosau Beds of Glanegg, Austria; E-F is from the Coniacian Craie de Villedieu of La Ribochère, Loir-et-Cher, France. A-B, I $\times 2$; C-D, E-F $\times 1$; G-H $\times 4$.



Fig. 3. *Paratexanites serratomarginatus* (Redtenbacher). A. Paralectotype, NS 6387. B. Lectotype, NS 6381. C. Paralectotype, NS 18428. D. Paralectotype, NS 6382. All specimens are from the Coniacian Gosau Beds of Glanegg, Austria. $\times 2$.

Discussion

The above description, based entirely on material from Glanegg, shows this species to be variable in both density and strength of ornament. A small, compressed specimen from Glanriedel, Austria, NHMW 1978/2029/3 (Fig. 4), is comparable to material from Glanegg. De Grossouvre (1894: 69, pl. 16 (fig. 1a-b) refigured herein as Fig. 7A-B) described a much larger specimen from the Craie de Villedieu of La Ribochère, Couture, Loir-et-Cher, France, which Matsumoto (1970: 263) has designated holotype of the subspecies *P. serratomarginatus grossouvrei*. Matsumoto (1970: 262) differentiated it from the Austrian form because of the 'stronger and more rounded inner ventrolateral

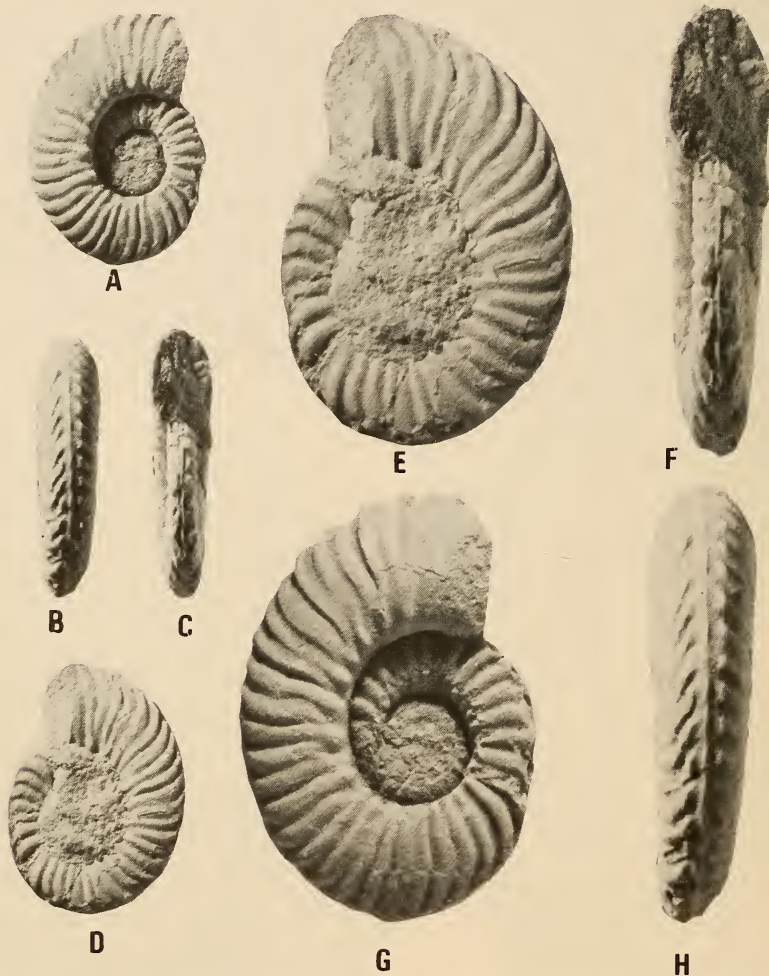


Fig. 4. *Paratexanites serratomarginatus* (Redtenbacher) NHMW 1978/2029/3 from the Coniacian Gosau Beds of Glanriedel, Austria. A-D $\times 1$; E-H $\times 2$.

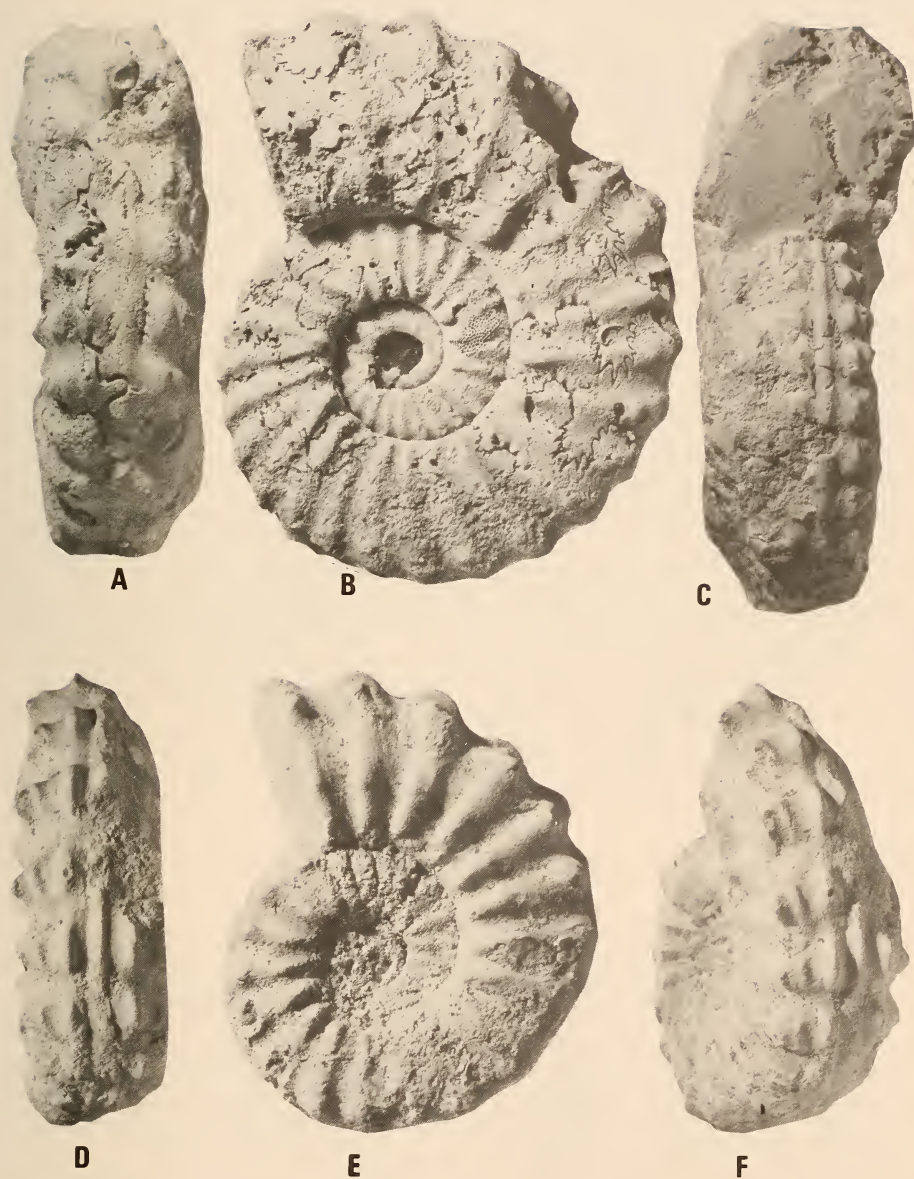


Fig. 5. *Paratexanites serratomarginatus* (Redtenbacher). A-C. FSR 'A', Seunes Collection. D-F. FSR 2834. Both specimens from the Coniacian Craie de Villedieu of La Ribochère, Loir-et-Cher, France. $\times 1$.

tubercles which are approximated to the outer ones, forming double ventrolateral major protuberances . . . the ventral keel shows weak undulations which correspond in number to the radial ribs, but in the Alpine species the keel is continuous and not undulated'. As the description of the Austrian material shows, the criterion of undulose v. continuous keel is not valid. Equally our largest and ontogenetically most advanced specimen (Fig. 2C-D) shows the double protuberance of the holotype of *P. serratomarginatus grossouvrei*, and there is such variation in the relative development of submarginal (3) and marginal (4) tubercles in the Austrian type series that this scarcely seems a criterion for separation.

The authors figure, however, three smaller French specimens from the Coniacian part of the Craie de Villedieu of La Ribochère (Figs 2E-F, 5A-F, 6) that show a greater range of variation and more advanced ontogenetic develop-

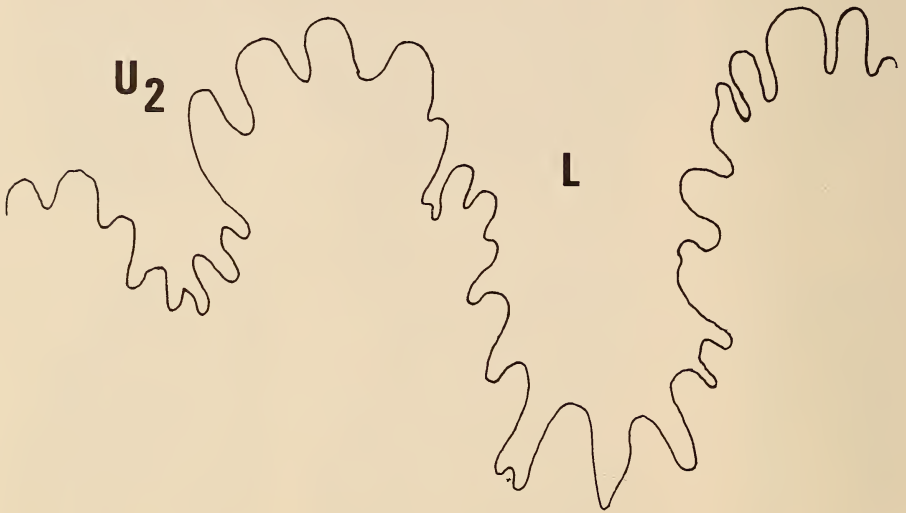


Fig. 6. *Paratexanites serratomarginatus* (Redtenbacher). External suture of FSR 'A', Seunes Collection. $\times 6$.

ment than is seen in the Austrian specimens. All are sparser ribbed than the lectotype, some with only half as many ribs at a somewhat greater diameter, although there is overlap in rib density with other types. FSR 'A' (Fig. 5A-C) is very close indeed to the Austrian type material, but FSR 2835 (Fig. 2E-F) is a curious, slowly expanding form with fewer ribs, which are more flexuous and have stronger bullae, with the marginal (4) tubercle very small indeed (Fig. 2E). FSR 2834 (Fig. 5D-F) shows similar features, especially the prominence of the submarginal (3) tubercle, while the marginal (4) tubercle is almost indistinguishable at the beginning of the last whorl, although strengthening towards the aperture. Given this variation and the overlap between the Austrian and

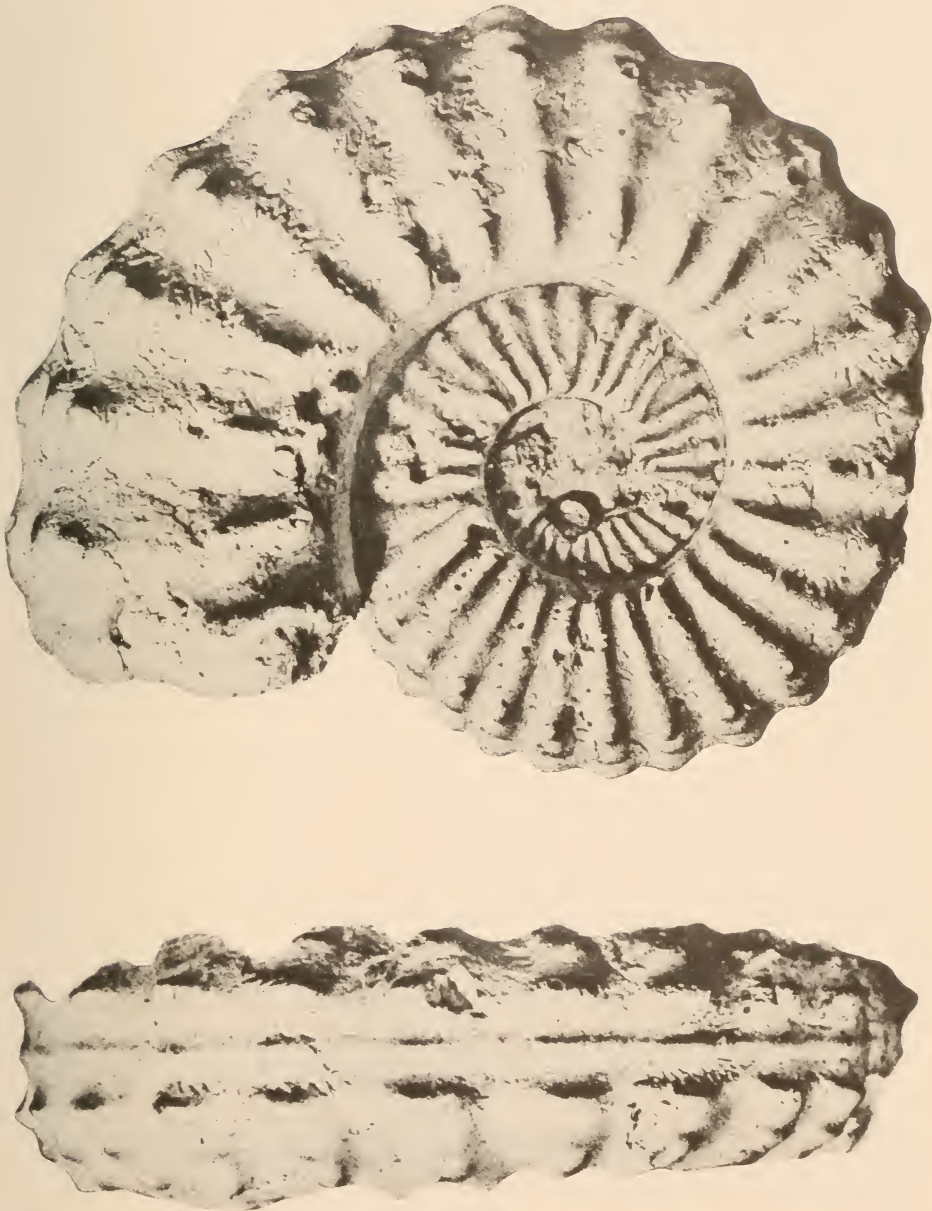


Fig. 7. The holotype of *Paratexanites serratomarginatus* (Redtenbacher) *grossouvrei* Matsumoto, from the Coniacian Craie de Villedieu of La Ribochère, Loir-et-Cher, France. Copy of De Grossouvre 1894, pl. 16 (fig. la-b). Reduced $\times 0.9$.

French specimens, we doubt that they merit subspecific separation, although acknowledging differences in variation range.

Specimens described from Japan by Matsumoto (1970: 260, pl. 36 (figs 1–3), text-fig. 16) fall into *P. serratomarginatus* as here interpreted. Collignon's (1966) specimens have a lateral tubercle and should be referred to *Plesiotexanites*, while we would continue to refer to the Zululand material (Klinger & Kennedy 1980a: 59, figs 45–47A) as *Paratexanites* sp. aff. *P. serratomarginatus*.

When compared to other 'Parabevahites', *Paratexanites emscheris* (Schlüter, 1876: 155, pl. 42 (figs 8–10)) has coarser, straighter ribs and umbilical bullae low on the flank rather than perched on the umbilical shoulder, and there are other differences as noticed by Matsumoto (1970: 262). *Paratexanites sellardsi* Young (1963: 79, pl. 32 (fig. 7), pl. 36 (figs. 3–5), pl. 37 (fig. 1), pl. 39 (fig. 4), pl. 49 (fig. 3), text-fig. 17) is also more coarsely ribbed and robustly tuberculate.

Occurrence

The type specimens are from Glanegg, Austria. Other ammonites from this locality (Brinkmann 1935: 2; Kennedy & Summesberger, in preparation) include *Gaudryceras glaneggense* (Redtenbacher), *Otoscaphtes arnaudi* (De Grossouvre), 'Ammonites' *aberlei* Redtenbacher, *Gauthiericeras margae* (Schlüter), and *Protexanites* sp. juv. These suggest a stratigraphic level way above the base of the Coniacian stage. The species is also recorded from France, Tunisia and Zululand and, where reliably dated, is also of Coniacian age.

Texanites quinquenodosus (Redtenbacher, 1873)

Figs 8–16

Ammonites texanus von Hauer (*non* Roemer, 1852) 1858: 10, pl. 2 (figs 4–6).

Ammonites quinquenodosus Redtenbacher, 1873: 108, pl. 24 (fig. 3a–b).

Mortoniceras texanus Schlüter sp.: Zurcher, 1905: 686.

Mortoniceras quinquenodosum (Redtenbacher): Yabe & Shimizu, 1923: 30 (*partim*).

Mortoniceras quinquenodosum [*lapsus*] (Redtenbacher): Diener, 1925: 147 (*partim*).

?*Texanites quinquenodosus* var. *evoluta* Haas, 1942: 18, text-fig. 12.

Texanites quinquenodosus (Redtenbacher): Collignon, 1948: 69, text-fig. 2; ?1966: 128, pl. 510 (fig. 2021). Thomel, 1969: 12, pl. G (figs 1–2). Klinger & Kennedy 1980a: 135, figs 102–3.

Texanites (*Texanites*) *quinquenodosus* (Redtenbacher): Matsumoto, 1970: 272. Wiedmann, 1979: 48, pl. 7 (figs C–D).

Texanites aff. *quinquenodosus* (Redtenbacher): Fabre-Taxy, 1963: 17, pl. 1 (fig. 14).

Texanites (*Texanites*) sp. aff. *T. (T.) quinquenodosus* (Redtenbacher): Matsumoto, 1970: 273, pl. 42 (fig. 3a–b), pl. 46 (figs 1–3).

Type

The lectotype is GBA 1873/01/13, the original of Redtenbacher 1873, pl. 24 (fig. 3a–b), from the Santonian Gosau Beds of St Wolfgang, Ischl, Austria.

Other specimens studied

In addition to the lectotype, the following specimens were available: LL 41/1938, a paralectotype, from the Schneiderwirtsbrücke, Ischl; LL 32 from Gosau; GBA 1873/01/13 (SV 2569), a paralectotype from Gosau; NHMW 1935.III.39, from Grabenbach, Gosau; NHMW 1926.II.2469, from the Nefgraben, Russbach, Gosau; NHMW 1935.III.40, from Gosau; GBA, an unregistered fragment from Gosau, and a possible paralectotype; NHMW 1935.III.41, from Gosau; and Böhm Collection from the Nefgraben, Gosau. All specimens are of Santonian age.

Dimensions

	<i>D</i>	<i>Wb</i>	<i>Wh</i>	<i>Wb:Wh</i>	<i>U</i>	<i>R</i>
NHMW 1935.III.40	118,5	32(27)	40(34)	0,8	51(43)	27

Description

The lectotype (Fig. 8) is a flattened and distorted internal mould with almost a whorl of body chamber preserved, and a maximum diameter of almost 160 mm. Coiling is very evolute, the inner whorls being exposed to the outer ventrolateral (4) tubercle, which is housed in a small notch in the umbilical wall of the succeeding whorl. In the best preserved specimen, NHMW 1935.III.40 (Figs 12–13, 14A), the broad, shallow umbilicus comprises 43 per cent of the diameter. Uncrushed specimens show the intercostal whorl section to have been high oval with convergent flanks and a breadth to height ratio of 0,75. The costal section is also compressed, with the maximum width at the lateral (2) tubercle, and a breadth to height ratio of 0,87.

Ornament consists of numerous (27–32) straight, simple, recti- to slightly prorsiradiate ribs. These arise at the umbilical seam, and bear a pointed umbilical (1) bulla directed into the umbilicus. There are a larger, feebly clavate lateral (2) tubercle, a larger, clavate submarginal (3) tubercle and a strong clavate marginal (4) tubercle, and a long external (5) tubercle, which tends to link with its neighbours into an undulose keel. There is a strong, faintly undulose siphonal keel flanked by distinct grooves (Fig. 14A–B).

On adult body chambers (e.g. LL 41/1938 (Figs 15–16)), the tubercles decline and the ribs crowd towards the aperture.

The suture line is quite simple (Fig. 11) with moderately incised elements.

Discussion

Specimens available vary somewhat in strength and number of ribs while, when shell is preserved, the tubercles are also much sharper than on moulds during early growth (Figs 9–10), and there are strong transverse growth striae in adults (Figs 15–16).

Matsumoto (1970: 273, pl. 42 (fig. 3), pl. 46 (figs 1–3)) has described a series of specimens from the Lower Santonian of Hokkaido, Japan, which shows developmental stages at much smaller sizes than seen in the Austrian



Fig. 8. *Texanites quinquenodosus* (Redtenbacher). The lectotype, GBA 1873/01/13, the original of Redtenbacher 1873, pl. 24 (fig. 3a) from the Santonian Gosau Beds of St Wolfgang, Austria. $\times 1$.



Fig. 9. *Texanites quinquenodosus* (Redtenbacher). Paralectotype, GBA 1873/01/13 (SV 2569), the original of Redtenbacher 1873, pl. 24 (fig. 3a-b) from the Santonian Gosau Beds of St Wolfgang, Austria. A-C $\times 1$; D $\times 2$.



Fig. 10. *Texanites quinquenodosus* (Redtenbacher). A-C. NHMW 1935. III. 41, from the Santonian Gosau Beds of Gosau, Austria. $\times 1$.

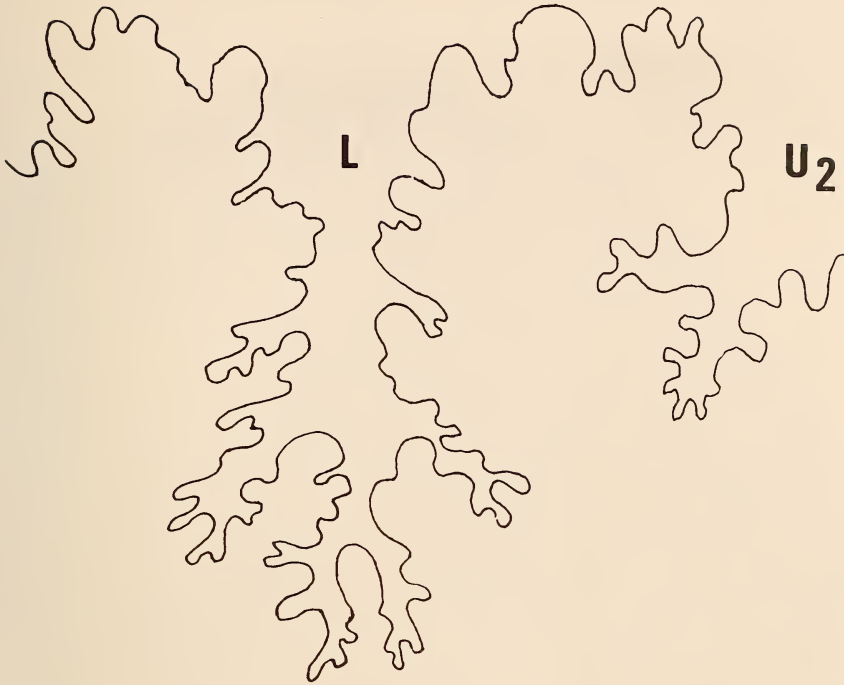


Fig. 11. *Texanites quinquenodosus* (Redtenbacher). External suture of GBA 1873/01/13 (SV2569). $\times 6$.

material. The large specimens from Japan are said to differ from the lectotype in having the ventral (=external (5)) clavus displaced in front of the outer ventrolateral, but this is seen to some degree in GBA 1873/01/13 (SV 2569) (Fig. 9A–B, D), and is probably of limited significance.

Texanites quinquenodosus most closely resembles *Texanites collignoni* Klinger & Kennedy, 1980a (= *Texanites oliveti* non Blanckenhorn sensu Collignon 1948, 1966; Matsumoto & Ueda 1962; Pop & Szasz 1973; Matsumoto 1978) from the Lower Santonian of Madagascar, Zululand, Japan, Romania, and possibly North America. The two species have comparable dimensions and rib densities on the outer whorls, but differ mainly in details of ornamentation. In *T. quinquenodosus* tuberculation is distinctly clavate, especially in the early stages of growth, whereas *T. collignoni* has more spinose ornament throughout. Furthermore, crowding of ribbing and decline of tuberculation towards the body chamber is not as common in *T. collignoni* as in *T. quinquenodosus*. Given more material with precise stratigraphic data, and taking the effects of differential preservation and intraspecific variation into account, specific separation of the two may prove unnecessary. For the present, however, the clavate tuberculation in *T. quinquenodosus* is regarded as being sufficient to separate it from *T. collignoni*.



Fig. 12. *Texanites quinquenodosus* (Redtenbacher). NHMW 1935. III.40, from the Santonian Gosau Beds of Gosau, Austria. $\times 1$.



Fig. 13. *Texanites quinquenodosus* (Redtenbacher). NHMW 1935.III.40, from the Santonian Gosau Beds of Gosau, Austria. $\times 1$.



Fig. 14. *Texanites quinquenodosus* (Redtenbacher). A. NHMW 1935.III.40, from the Santonian Gosau Beds of Gosau. B. Paralectotype, LL 41/1938, from Schneiderwirtsbrücke Ischl. A. $\times 1$; B $\times 0,75$.



Fig. 15. *Texanites quinquenodosus* (Redtenbacher). Paralectotype LL 41/1938, from the Santonian Gosau Beds of Schneiderwirtsbrücke, Ischl. $\times 0,75$.



Fig. 16. *Texanites quinquenodosus* (Redtenbacher). Paralectotype, LL 41/1938, from the Santonian Gosau Beds of Schneiderwirtsbrücke, Ischl. $\times 0,75$.

Texanites oliveti (Blanckenhorn, 1905), according to the interpretation of Klinger & Kennedy (1980a), is a distinctly compressed, Upper(?) Santonian species.

T. quinquenodosus may be separated from *Texanites texanus texanus* (Roemer) (see Young 1963: 80, pl. 38 (figs 1–2), pl. 40 (figs 1–3), pl. 41 (fig. 4), text-figs 21g, 22a, 25d) by its more evolute coiling and denser ribbing; these also distinguish it from *T. texanus twiningi* Young (1963: 82, pl. 38 (fig. 5), pl. 39 (fig. 1), pl. 41 (figs 2,5), pl. 48 (fig. 4)). *Texanites texanus gallicus* Collignon (1948: 75, pl. 8 (fig. 1–1a); De Grossouvre 1894: 80, pl. 16 (figs 2, 3a–b, 4a–b), pl. 17 (fig. 1)) is less compressed, and has the inner three rows of tubercles rounded. In *T. texanus hispanicus* Collignon (1948: 76, text-fig. 11–11a, pl. 8 (fig. 2–2b)) there are comparable differences, and the lateral tubercle migrates ventrally until it reaches a mid-flank position.

The Angolan *Texanites quinquenodosus evolutus* Haas (1942: 18, text-fig. 12) has an umbilical diameter of 53 per cent compared to 43 in the best preserved Gosau specimen, and can only very doubtfully be referred to Redtenbacher's species. Similarly, the specimen described as *T. quinquenodosus* from Madagascar (Collignon 1966: 128, pl. 510 (fig. 2021)) is a doubtful representative by virtue of its tighter coiling and more compressed whorl section.

Occurrence

The Austrian specimens can be dated no more precisely than Santonian in our present state of knowledge. The species is also recorded from the Lower Santonian of south-eastern France, Hokkaido (Japan) and, doubtfully, from the Santonian of Angola and Upper Santonian of Madagascar.

INTRASPECIFIC VARIATION IN *Reginaites zulu* KLINGER & KENNEDY, 1980, AND HOMOEOMORPHY WITH *Plesiotexanites (P.) stangeri* (BAILY, 1855)

(By H. C. Klinger & W. J. Kennedy)

In the authors' (Klinger & Kennedy 1980a) description of the South African representatives of the ammonite subfamily Texanitinae, two new species definitely referable to the genus *Reginaites* Reyment, 1957, were erected: *Reginaites zulu* and *Reginaites reymenti*.

Recent collecting at the type locality of *R. zulu* yielded additional material that allows the authors to comment on the intraspecific variation in the species and firmly to date it as Upper Santonian on the basis of its association with *Inoceramus (Cordiceramus) muelleri* Petrascheck. It also demonstrates a striking homoeomorphy with the partly contemporary (though apparently geographically separated) species *Plesiotexanites (P.) stangeri* (Baily, 1855). The

material further supports the authors' inclusion of *Reginaites* in the subfamily Texanitinae, rather than in the subfamily Peroniceratinae Hyatt, as advocated by Matsumoto (1965: 238) and Wiedmann (1978: 670).

Reginaites zulu Klinger & Kennedy, 1980

Figs 17–25

Reginaites zulu Klinger & Kennedy, 1980a: 116, figs 90–92, 93A–B, 94.

Types

The holotype by original designation is SAS–H126A/9 from Bed A at locality 105 on the south-eastern shores of False Bay, Zululand, St Lucia Formation, Upper Santonian. Paratype SAS–H126A/4 is from the same horizon and locality.

Material

Five specimens, SAM–PCZ5952–6, all from the same locality and horizon as the types.

Dimensions

	<i>D</i>	<i>Wb</i>	<i>Wh</i>	<i>Wb:Wh</i>	<i>U</i>	<i>R</i>
PCZ5955	75,0	25,0(33,3)	26,0(34,7)	0,96	36,0(48,0)	18
at	134,0	34,0(25,4)	35,0(26,1)	0,97	74,0(55,2)	11 × 2
PCZ5953	120,0	32,0(26,7)	34,0(28,3)	0,94	62,0(51,7)	23
H126A/9	140,0	38,7(27,6)	40,0(28,6)	0,96	74,0(52,9)	21
PCZ5956	195,0	—	56,0(28,7)	—	105,0(53,8)	—

Description

Coiling is very evolute with an umbilical diameter varying between 48 and 55 per cent, increasing with growth. The whorl section changes through ontogeny, being subsquare on the inner whorls, becoming compressed subrectangular with a fastigiate venter, and then distinctly compressed with a conspicuous central keel and subordinate lateral keels (Fig. 17A).

None of the specimens has the innermost whorls preserved, but in SAM–PCZ5953 (Fig. 18) ornament at approximately 40 mm diameter already consists of pinched umbilical (1) bullae situated at the umbilical edge, and broad, low, prorsiradiate ribs bearing very large, bullate to clavate elongated ventrolateral (3 + 4) tubercles situated a little distance away from the umbilical seam of the succeeding whorl. The venter at this stage is already distinctly tricarinate, with the central keel strongest. Strength and density of ribbing is extremely variable, as the Figures show.

Division of the ventrolateral tubercle takes place at varying diameters. In SAM–PCZ5953 (Fig. 18) definite signs of division are already present at a diameter of approximately 50 mm, whereas in the holotype this becomes noticeable only at a diameter of 65 mm (Figs 19–20). With increasing diameter

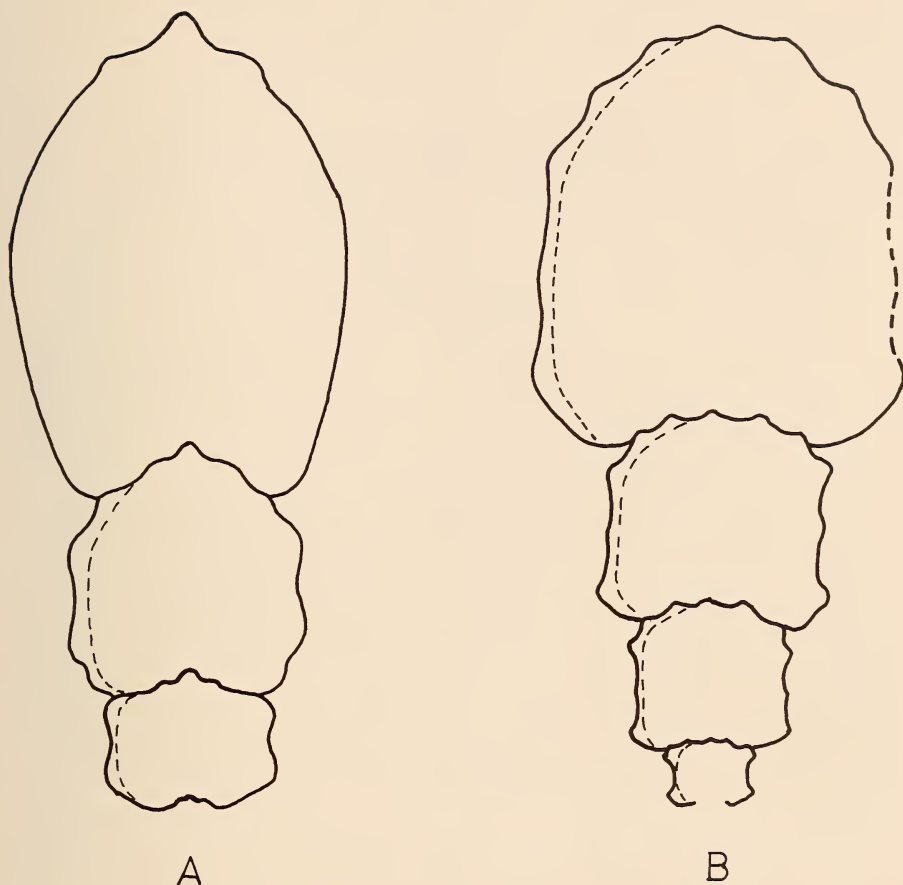


Fig. 17. A. *Reginaites zulu* Klinger & Kennedy, 1980, illustrating ontogenetic changes in whorl section (after Klinger & Kennedy 1980a, fig. 90A). B. *Plesiotexanites (P.) stangeri* (Bailey, 1855) illustrating ontogenetic changes in whorl section (after Matsumoto 1970, text-fig. 23b). All $\times 1$.

this separation becomes more obvious, resulting in a clavate marginal (4) tubercle, situated slightly forward of a larger, rounded submarginal (3) tubercle (Figs 20A–B, 21C–D). Concurrent with division of the ventrolateral tubercle, all lateral ornament weakens, the ratio of whorl breadth to whorl height decreases, and the venter becomes distinctly fastigiate. Differences in strength of ornament and stage at which attenuation takes place is variable. SAM-PCZ5956 (Fig. 22) shows attenuation of ornament and change in whorl section to the point where the flanks of the last part of the phragmocone are smooth. On body chambers (Figs. 21A–B herein) (Klinger & Kennedy 1980a, fig. 94A–B) lateral ornament is reduced to indistinct broad, low swellings.



Fig. 18. *Reginaites zulu* Klinger & Kennedy, 1980. SAM-PCZ5953 from locality 105, St Lucia Formation, Zululand. $\times 1$.



Fig. 19. *Reginaites zulu* Klinger & Kennedy, 1980. The holotype, SAS-H126/9, from locality 105, St Lucia Formation, Zululand. $\times 1$.



Fig. 20. *Reginaites zulu* Klinger & Kennedy, 1980. The holotype, SAS-H126/9, from locality 105, St Lucia Formation, Zululand. $\times 1$.



Fig. 21. *Reginaites zulu* Klinger & Kennedy, 1980. A-B. SAM-PCZ5952, a body chamber fragment illustrating total disappearance of ornament. C-D. SAM-PCZ5954 illustrating division of ventrolateral tubercle. Both specimens from locality 105, St Lucia Formation, Zululand. $\times 1$.



Fig. 22. *Reginaites zulu* Klinger & Kennedy, 1980. SAM-PCZ5956 illustrating ontogenetic change in ornament. From locality 105, St Lucia Formation, Zululand. $\times 0,5$.

None of the specimens shows distinct lateral (2) tubercles at any stage of ontogeny, although SAM-PCZ5955 (Fig. 23) has faint swellings on the central part of the ribs on the inner whorls. Preservation is poor, and we cannot confirm that these are incipient lateral (2) tubercles or not. In only three specimens are part of the suture exposed: it is rather simple (Fig. 24) but varies considerably in details and the width of the lateral lobe (L).

Discussion

With only the holotype and a fragment of body chamber of *Reginaites zulu* at their disposal, the authors (Klinger & Kennedy 1980a) were initially

impressed by the strong ornament on the inner whorls of the phragmocone and the lack of ornament on the body chamber, and failed to recognize the resemblance of the species to *Plesiotexanites (P.) stangeri* (Baily, 1955). The new material shows that there is remarkable similarity, and that the two species may be closer related than previously suspected. (Young 1963: 93 had also



Fig. 23. *Reginaites zulu* Klinger & Kennedy, 1980. SAM-PCZ5955, specimen with sparse costation, comparable with *Plesiotexanites (P.) stangeri* 'var. *sparsicosta*' Spath. From locality 105, St Lucia Formation, Zululand. $\times 1$.

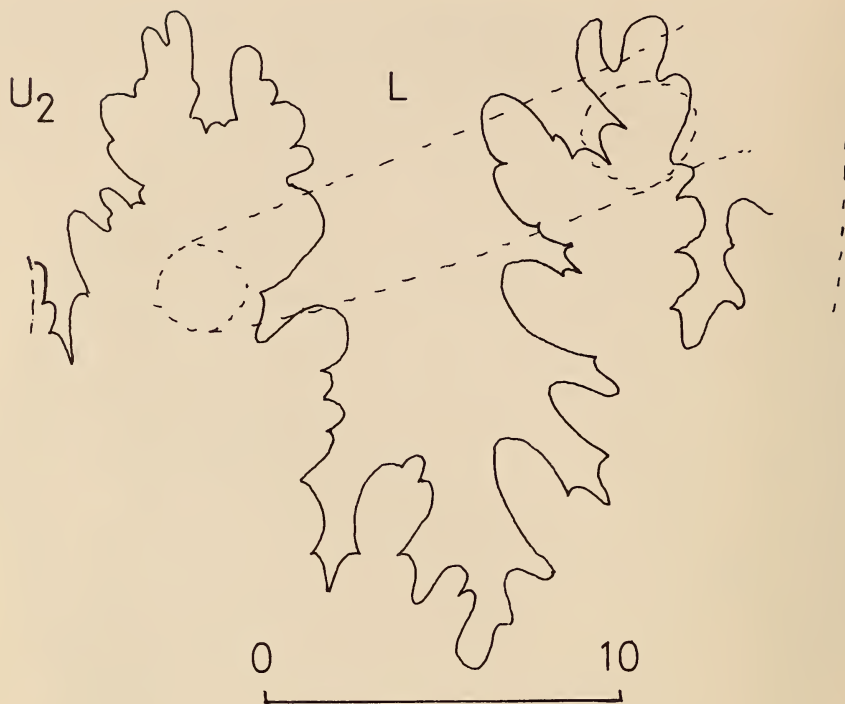


Fig. 24. *Reginaites zulu* Klinger & Kennedy, 1980. Part of external suture of SAM-PCZ5956. Millimetre scale bar for size.

commented on similarities between *Reginaites durhami* Young and *Plesiotexanites* (*P.*) *stangeri*). In addition, this is the largest assemblage of *Reginaites* known, most other species being monotypic.

The ontogenies of *R. zulu* and *P. (P.) stangeri* are very similar, although the accompanying changes in ornament and whorl section are much more strongly expressed in the former. These changes involve development of tuberculation on the inner whorls, gradual effacement of all ornament on the outer phragmocone whorls and body chamber, and change in whorl section.

In the very early stages, *R. zulu* and *P. (P.) stangeri* differ only in ventral ornament. *R. zulu* is distinctly tricarinate, whereas *P. (P.) stangeri* is unicarinate, with a pair of spirally elongated external (5) tubercles.

In both species the ventrolateral (3 + 4) tubercle, which is situated in the umbilical seam, is enlarged in *Protexanites* (*Protexanites*) fashion in early stages of growth. At varying diameters this ventrolateral tubercle starts dividing into two, resulting in a clavate marginal (4) and a generally rounded submarginal (3) tubercle—the so-called '*Parabevahites*' stage. The *Paratexanites*-like stage, in which total separation of these tubercles takes place, is completed in both species, generally with the marginal (4) tubercle situated slightly ahead of the



Fig. 25. *Plesiotexanites (P.) stangeri* (Baily, 1855). Cast of holotype, BMNH C73333, from Umzamba estuary, Pondoland. $\times 0,43$.

submarginal (3) one. While the separation of the ventrolateral tubercle takes place in *P. (P.) stangeri*, a lateral (2) tubercle appears, thus completing the pentatuberculate *Texanites*-like stage. The stage of appearance, strength and persistence of the lateral (2) tubercle in *P. (P.) stangeri* is very variable. The lateral tubercle may be faint throughout, or persist only for a short time before being absorbed into the ribbing. As far as *lateral* ornament is concerned, the only difference between *P. (P.) stangeri* and *R. zulu* is the variable appearance

of a lateral (2) tubercle in the former. The venters, however, remain different throughout.

Apart from relative strength of ornament at comparable stages of development (which may partially be explained by differential preservation), *R. zulu* and *P. (P.) stangeri* show comparable intraspecific variation in density of ribbing, which has led to the usage of varietal names *sparsicosta* and *densicosta* in the latter species (e.g. Spath 1921: 138, pl. 5 (figs 1–2)). In *P. (P.) stangeri* these differences in density of ribbing appear to be restricted mainly to the inner whorls, whereas in *R. zulu* they are noticeable to greater diameters.

In both species ornament weakens during ontogeny, although the reduction is more prominent in *R. zulu* than in *P. (P.) stangeri*. The new material referable to *R. zulu* (Fig. 22) shows that parts of the phragmocone may already be devoid of ornament, whereas the body chamber is completely smooth, except for low, broad, undulating swellings (Fig. 21A–B herein) (Klinger & Kennedy 1980a Fig. 94A–B). In *P. (P.) stangeri* a similar weakening takes place, but in the holotype the largest specimen as yet obtained of the species, the body chamber (which consists of one whorl here) still bears faint, though discernible lateral ornament (Fig. 25).

There are also comparable ontogenetic changes in whorl section (Fig. 17A–B). Both species are initially depressed, quadrate to rectangular, but whorl height gradually increases over whorl breadth, so that the section is eventually distinctly compressed. The venter becomes fastigiate in both species, but in *R. zulu* this is enhanced by the lateral keels.

Phylogenetic relationships between *R. zulu* and *P. (P.) stangeri* are not clear, but the ontogenetic changes in both species are too similar to consider them to be entirely those of homoeomorphs. *P. (P.) stangeri* occurs mainly in the Upper Santonian of Pondoland, but has also been recorded from the Middle Santonian of Madagascar, and Young (1963: 22) even records it as early as the lowest parts of the Lower Santonian of the Gulf Coast of North America. *R. zulu* occurs in Zululand in association with *Inoceramus (Cordiceramus) muelleri* Petrascheck, but below the first occurrence of *Submortoniaceras*, which places it in the uppermost part of the Santonian. Because of similarities of ornament on the inner whorls of *R. zulu* and *Plesiotexanites (P.) matsumotoi* Klinger & Kennedy, 1980a, it seems feasible to derive *R. zulu* from the latter (probably via *Reginaites reymenti* Klinger & Kennedy, 1980a) in the Upper Santonian, rather than directly from *P. (P.) stangeri*. However, the parallel changes in ontogenetic development of *R. zulu* and *P. (P.) stangeri* are so striking that we can perhaps trace their ancestry to a common origin somewhere in the Lower Santonian.

Palaeobiogeographic data should be interpreted with caution on the basis of this limited material but, to date, the great majority of specimens of *P. (P.) stangeri* have been reported from the transgressive shallower water sediments of the Umzamba Formation, whereas all known specimens of *R. zulu* have been found in the deeper water sediments of the St Lucia Formation of Zululand.

Differences between *R. zulu* and other species of *Reginaites* were given earlier (Klinger & Kennedy 1980a), and are here briefly repeated: *R. quadrituberculatum* Reyment, 1957, *R. leei* (Reeside, 1927), *R. durhami* Young, 1963, *R. reymenti* Klinger & Kennedy, 1980a, and *R. gappi* Wiedmann, 1978, all have a lateral tubercle at some stage. '*Reymentites*' *hatai* Matsumoto, 1965, has the umbilical tubercle displaced on the flanks.

All these data support the authors' (Klinger & Kennedy 1980a) and Young's (1963) views of placing the genus *Reginaites* in the subfamily Texanitinae, rather than in the subfamily Peroniceratinae.

COLOUR-BANDING IN MICROMORPHS OF *Submorticeras woodsi*
(SPATH, 1921) AND THEIR HOMOEOMORPHY WITH *Protexanites*
(*P.*) *bontanti shimizui* MATSUMOTO, 1970.

(By H. C. Klinger & W. J. Kennedy)

Two small specimens of *Submorticeras woodsi* from the Santonian-Campanian sediments of Kwa-Mbonambi, Zululand (locality 6 of Kennedy & Klinger 1975: 282) are of interest in showing traces of colour bands in the preserved part of the shell, and in apparently being adult at diameters well below those of normal representatives of the species. They also show striking homoeomorphy with the stratigraphically older *Protexanites* (*P.*) *bontanti shimizui* Matsumoto, 1970.

Submorticeras woodsi s.l. (Spath, 1921)

Figs 26–27

Submorticeras woodsi s.l. (Spath): Klinger & Kennedy, 1980a: 242, figs 186–199, 200B (with synonymy).

Material

SAM-PCZ5957–8 both from an unspecified horizon near the Santonian-Campanian boundary at Kwa-Mbonambi (locality 6 of Kennedy & Klinger 1975: 282), St Lucia Formation, Zululand.

Dimensions

	<i>D</i>	<i>Wb</i>	<i>Wh</i>	<i>Wb:Wh</i>	<i>U</i>
PCZ5957	46,0	13,5(34,0)	18,5(40,2)	0,73	15,0(32,6)
PCZ5958 (crushed)	48,0	12,5(26,0)	17,0(35,4)	0,73	—

Description

Both specimens are less than 50 mm in diameter. PCZ5958 is crushed dorsoventrally, hence the umbilicus appears much narrower than that of PCZ5957.

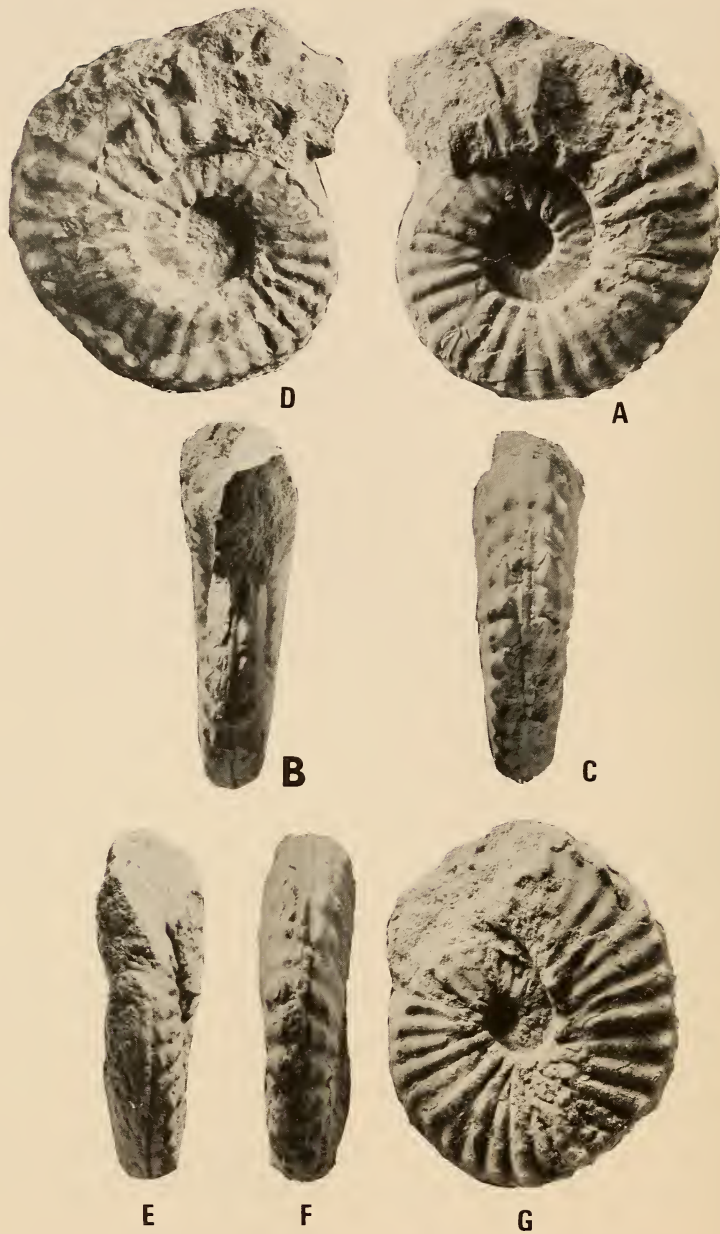


Fig. 26. *Submortoniceras woodsi* (Spath, 1921). A-D. SAM-PCZ5957. D without whitening to show parts of colour banding. E-G. SAM-PCZ5958, specimen crushed dorsoventrally. Both from locality 6, St Lucia Formation, Zululand. All $\times 1$.

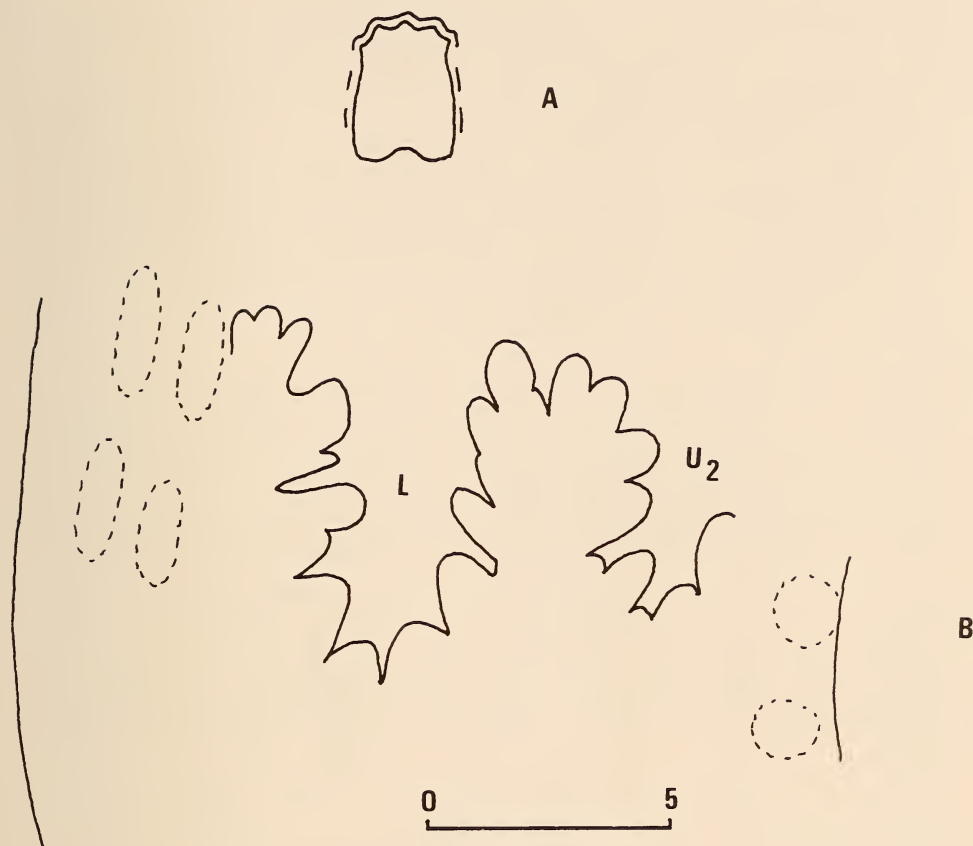


Fig. 27. *Submortoniceras woodsi* (Spath, 1921). A. Whorl section of SAM-PCZ5957 to illustrate distribution of colour banding, $\times 1$. B. External suture of SAM-PCZ5956, millimetre scale bar for size.

PCZ5957 (Fig. 26A–D) shows details of the ontogeny. At 5 mm diameter the flanks are still completely smooth; at 8 mm diameter umbilical (1) tubercles and bifurcating ribs are visible on the flanks. At 16 mm diameter weak lateral (2) and submarginal (3) tubercles appear on the flanks. A full texanite complement of 5 rows of tubercles and a median keel is visible at 25 mm diameter. The lateral (2) and submarginal (3) tubercles, however, are very weak, mimicking a *Protexanites* (*P.*)-like type of ornament. Ornament remains like this until near the apertural end, where the lateral (2) tubercle becomes slightly more prominent. The last half-whorl is non-septate and the last few septa overlap.

Part of the original aragonitic shell material is preserved. The inner shelly layer is creamy coloured with a reddish tint, whereas the outer layer is more

brownish. On the outer layer, two darker, sepia-coloured spiral bands are visible, one near the submarginal (3) tubercle (Fig. 26D). In addition, a distinct black substance occurs in the ventral area between the opposite rows of marginal (4) and external (5) tubercles in places. The distribution of colour bands is shown in Figure 27A.

PCZ5958 (Fig. 26E–G) is not as well preserved, but shows distinct pentatuberculate ornament at 25 mm diameter. The lateral (2) and submarginal (3) tubercles are again weaker than the others. Ornament weakens towards the later part of the phragmocone, but again becomes stronger on the body chamber. The last few septa are also crowded.

Discussion

Because of the weak development of the lateral (2) and submarginal (3) tubercles, and also because of the small size, these specimens are striking homoeomorphs of the stratigraphically older *Protexanites* (*P.*) *bontanti shimizui* Matsumoto, 1970 (compare Matsumoto 1970, pl. 31 (figs 1–2), text-fig. 6; 1971: 147, pl. 23 (fig 4), text-fig 10; Matsumoto & Hirano 1976: 335, pl. 35 (figs 1–4), text-fig. 2). Close examination, however, clearly shows the pentatuberculate ornament in the Zululand specimens. The two species also differ considerably in details of the suture lines (compare Fig. 27B herein with Matsumoto 1970, text-fig. 6) and cannot be confused with each other. Examination of the suture lines in the present material suggests closest affinity with the subspecies *Submortonicerias woodsi woodsi* as interpreted by Klingler & Kennedy (1980a: 252–3).

Matsumoto (1970: 238) had already commented on the similarity between *Protexanites* (*P.*) *bontanti* s.l. and some examples of *Submortonicerias*, e.g. *S. collignoni* (Shimizu); the latter a possible synonym of *S. woodsi* according to the authors (Klingler & Kennedy 1980a: 238). Matsumoto's observations are further enhanced by the present data.

The presence and distribution of the colour bands on the one specimen, PCZ5957, compares favourably with that described in *P. (P.) bontanti shimizui* by Matsumoto & Hirano (1976) and adds to the homoeomorphic resemblance. Unfortunately, our material is too poorly preserved to add to Matsumoto & Hirano's general comments on coloration in Texanitinae, but nevertheless represents yet another record of coloration in the subfamily.

The ontogenetic changes in ornament and the crowding of the last few septa suggest that these two specimens represent adult individuals. The question that now arises is the relationship of these micromorphs to the more commonly known large specimens (even the specimen considered as dwarfed by the authors (Klingler & Kennedy 1980a figs 198, 200B) is gigantic compared to the present material). If nutritional deficiency were to blame (compare Boletzky & Wiedmann 1978), the co-occurrence of 'normally sized' specimens, e.g. SAM-PCZ5897 (Klingler & Kennedy 1980a, fig. 192) at 226 mm diameter at the same locality would be a contradiction. Apart from differences in overall

size, the present specimens differ from contemporary *S. woodsi* only in having a lower whorl section, as comparison of dimensions shows:

	<i>D</i>	<i>Wb</i>	<i>Wh</i>	<i>Wb:Wh</i>	<i>U</i>	<i>U:E tbs</i>
PCZ5897	226.0	74.0(32.7)	92.0(40.7)	0.80	74.0(32.7)	25 : 34
PCZ5957	46.0	13.5(34.0)	17.0(35.4)	0.73	15.0(32.6)	26 : 36

It is possible that we are here dealing with sexual dimorphs, the 'normally sized' specimens being the female (macroconch) and the smaller form the male (microconch). Apart from the fact that this would be the first suggestion of sexual dimorphism in the ammonite subfamily Texanitinae, the implications on the systematics, especially in the genus *Submorticeras*, are disturbing. Matsu-moto (1959) and Klinger & Kennedy (1980a) have illustrated the bewildering extent of intraspecific variation in *Submorticeras chicoense*, and *S. woodsi* and *S. condamyi* respectively. Added to this is a very rapid rate of evolution, as exemplified by *S. woodsi* and *S. condamyi*, which makes it difficult to separate one chronospecies satisfactorily from another. Should sexual dimorphism be added to the list of variables in the systematics of the genus *Submorticeras*, global correlation may become even more tenuous than at present.

ACKNOWLEDGEMENTS

We thank Dr F. Stojaspal of the Geologische Bundesanstalt, Vienna; Mag. A. Sikora of the Haus der Natur, Salzburg; Dr H. Kohl of the Oberösterreichisches Landesmuseum, Linz; Dr J. Louail of the Faculté des Sciences, Paris; Dr M. K. Howarth and Mr D. Phillips, British Museum (Natural History), London; and Prof. Dr J. Wiedmann, Tübingen, for allowing us to study material in their care. We also thank F. and K. Böhm, private collectors in Salzburg, for allowing us to study their collections.

Assistance from the technical staff of the University Museum, Oxford; South African Museum, Cape Town; and Institut und Museum für Geologie und Paläontologie, Tübingen, is appreciated.

Financial aid to H. C. Klinger from the South African Council for Scientific and Industrial Research, and, during the tenure of a research fellowship, from the Alexander von Humboldt Foundation, and to W. J. Kennedy from the National Environment Research Council (Great Britain) is gratefully acknowledged.

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